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Seed development in the genus *Peperomia**

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(WITH PLATES 3-6 AND A TEXT FIGURE)

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GENERAL DISCUSSION

Whether the sixteen-nucleate embryo sac of *Peperomia* is to be regarded as primitive, depends upon the homologies assumed or proved for the various structures found in this unusual type of embryo sac. In view of this, and since no axial row of megaspores is formed, the first question that naturally arises is whether the first four nuclei in the embryo sac are the morphological equivalents of four megaspore nuclei.

It is quite generally agreed that the cells of the axial row in the nucellus formed by the division of the definitive archesporial cell in most Angiosperms are homologous with those having a similar development in Gymnosperms; in both cases they are almost universally known as megaspores. There exists a further homology, although not quite so close, between the megaspores of Angiosperms and Gymnosperms and those of the heterosporous Pteridophytes. The tetrads of microspores, also, in all of these groups are homologous with one another, and, in a slightly different degree, with the megaspores in the same group. The evidence for these views has been well presented by Strasburger (73, 75), Overton (55, 56), Juel (36), Körnicke (40), Coulter (13), and others.

That the first four nuclei in the embryo sac of *Peperomia* are homologous with megaspore nuclei seems equally clear. The following facts indicate the correctness of this conception:

(1) The cell, the nucleus of which gives rise to these first four nuclei, may be considered, without valid objection, a megaspore mother-cell. It is developed in the position of the axial row. It is derived from a single primary archesporial cell, which cuts off

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a single tapetal cell. In fact, its position and whole antecedent development, being so closely similar to that so generally found in Angiosperms, constitute a strong bit of positive evidence for the view that it is a megaspore mother-cell.

(2) As is evidenced by the occurrence of synapsis in the nucleus of the definitive archesporial cell, preceding its division, the two divisions by which these four nuclei are formed are the reduction divisions, as is the case in the last two divisions in the formation of the megaspore nuclei in all other plants in which they are formed—so far as they have been investigated. In rare cases like that of *Alchemilla speciosa* (Murbeck, 53, 54; Strasburger, 74), in which apparent megaspore-formation occurs without reduction of chromosomes, there is no sexual fusion in the initiation of the embryo which is later developed in the embryo sac. Therefore, as Strasburger contends, such abnormal cases can not be considered examples of true megaspore-formation. The presence of the reduction divisions is considered by some workers as sufficient evidence for the acceptance of the theory of the homology of the megaspores of Angiosperms with those of the Gymnosperms and the higher Pteridophytes. It should mean as much in *Peperomia* as it does elsewhere in heterosporous plants.

(3) The tetrahedral arrangement of these first four nuclei points more strongly to the homology in question than does the linear tetrad, or axial row, arrangement, which occurs in nearly all seed-plants, both Gymnosperms and Angiosperms—since a tetrahedral arrangement of the microspores is found in nearly all heterosporous plants and in the megaspores of all heterosporous Pteridophytes. The linear tetrad of megaspores is universal in the Cycadales, the Coniferales, and the Ginkgoales, in all investigated cases known to the writer; but Juel (36) found a close approach to the tetrahedral arrangement in the megaspores of *Larix sibirica* as a general rule, the typical axial row being seldom found. The tetrahedral arrangement of megaspores is not altogether unknown in Angiosperms, having been observed in *Fatsia japonica* by Ducamp (17). Transitions between the axial row and the tetrahedral arrangement have been observed in *Aralia racemosa* by Ducamp (17), in *Garcinia* by Treub (77), in *Burmannia Championii* by Ernst and Bernard (22), in *Cynomorium*

by Juel (37), and in *Smilacina stellata* by McAllister (45). The case of *Smilacina* is particularly interesting here since the four megaspores show various transitions between the typical axial row and the tetrahedral arrangement. Moreover, after the megaspores are formed and unmistakably separated by walls, the walls disappear. The megaspore nuclei now become the first four nuclei of the embryo sac, and at this stage they assume the tetrahedral arrangement very similar to that in the four-nucleate embryo sac of *Peperomia*. It is not only in *Peperomia* that the first four nuclei of the embryo sac are arranged tetrahedrally, but this is likewise true in all genera in which sixteen free nuclei are formed in the embryo sac—namely, in *Gunnera* (Schneegg, 64; Ernst, 20, 21; Modilewski, 48; Samuels, 59), in *Sarcocolla* (Stephens, 70), in *Brachysiphon* (Stephens, 70), in *Penaea* (Stephens, 70), and in *Euphorbia* (Modilewski, 49, 51, 52).

(4) The fact that the tetrad is always complete in number of nuclei in *Peperomia* makes the homology seem rather more probable in this genus than it is in plants in which the axial row is incomplete, as for example, in one consisting of three cells instead of four.

(5) Eleven species of *Peperomia* have been shown to have sixteen nuclei in the mature embryo sac. In addition to the six here investigated are: *P. pellucida* (Campbell, 6), *P. hispidula* (Johnson, 34), *P. Sintenisii*, *P. arifolia*, and *P. Ottoniana* (Brown, 4). No species has been found to have any other number. As Brown (4) points out, the presence, in the mature embryo sac of *Peperomia*, of the larger number of nuclei than in the sac of ordinary Angiosperms, is in harmony with the view that more megaspore nuclei are concerned in the formation of the *Peperomia* type of embryo sac.

(6) The fact that all four nuclei divide, or germinate, can not militate against the theory that they are homologous with megaspore nuclei, because there are cases in which megaspores are undoubtedly formed and in which they all germinate—that is, the nuclei all divide. This is true, for example, in *Crucianella* (Lloyd, 41), in *Smilacina stellata* (McAllister, 45), and sometimes in *Epipactis* (Brown & Sharp, 5). And then there are intermediate cases in which one or more of the non-functional mega-

spore nuclei divide, e. g. in *Cercis Siliquastrum*, *Phaseolus multiflorus*, and *Erythrina Crista-galli*—all three investigated by Guignard (24). Another interesting case of this kind was found in *Scilla* (McKenney, 46).

(7) That all four nuclei take part in the formation of one embryo sac can not constitute a valid objection to the view, because there are cases where megaspores are undoubtedly formed and in which all four participate in the formation of one embryo sac, as in *Smilacina stellata* (McAllister, 45), and sometimes in *Epipactis* (Brown & Sharp, 5), the walls following the first two divisions of the megaspore mother-cell being evanescent in both cases. In the former case the megaspores are frequently arranged in an axial row, but as was mentioned above, the arrangement is very often an intermediate condition between the axial row and the tetrahedral arrangement, while in *Epipactis* the megaspores always have the linear arrangement.

In *Euphorbia procera* and *E. palustris* (Modilewski, 49, 52) and in the Penaeaceae (Stephens, 70), the quadripolar grouping of the nuclei in the mature embryo sac furnishes a strong bit of evidence that the embryo sac in each of these cases is a composite structure derived from the equivalents of four megaspore nuclei. The same may be true of *Peperomia*, which has the same number of nuclei in the mature embryo sac, even though the nuclei do not have the quadripolar grouping.

(8) Another significant piece of evidence is that there is a resting period following the second division in the embryo sac—that is, following the four-nucleate stage. This was observed in every species of *Peperomia* which was sufficiently studied. As is well known, a resting stage following the formation of the four megaspores is almost universal in plants. So, this phenomenon is in harmony with what would be expected.

(9) One of the strongest pieces of evidence favoring this view is the appearance of evanescent walls following the first and second divisions in the embryo sac of *Peperomia*—together with the fact that these walls have never been seen in the eight-nucleate embryo sac—that is, following the third division. These walls were first reported by Brown (4) in *Peperomia Sintenisii* and in *P. arifolia*. They have been seen by the writer in seven other

species of *Peperomia*, namely: *P. reflexa*, *P. verticillata*, *P. scandens*, *P. Fraseri* var. *resediflora*, *P. blanda*, *P. galioides*, and *P. Langsdorffii*(?). Similar evanescent separating walls occur in *Smilacina stellata* (McAllister, 45) and in *Epipactis* (Brown & Sharp, 5), in which cases it is plain that they are megaspore walls. Wiegand (79) reports an evanescent wall between the first two nuclei in the embryo sac of *Convallaria*, in which case there are no degenerating megaspores, but the definitive archesporial cell forms the embryo sac directly, and this wall very probably represents a megaspore wall. In this case, however, only the heterotypic division is followed by an evanescent wall.

The appearance of separating walls is, however, not absolutely essential in the formation of megaspores in cases where it is generally admitted that megaspores occur, *e. g.* the walls usually do not appear in *Crucianella* (Lloyd, 41), or in *Asperula* (Lloyd, 41), and sometimes not in *Eichhornia* (Smith, 68) or *Avena* (Cannon, 10). In each of these cases, however, the embryo sac develops from a single megaspore nucleus, while the others degenerate, regardless of the absence of walls. But, since separating walls do generally appear between the megaspore nuclei in other plants, their presence in *Peperomia* certainly strongly favors the homology.

Another explanation of the occurrence of these walls, in harmony with Campbell's (7) view, was suggested by Brown (4) and immediately rejected. He says: "If the walls corresponded to those of prothallial cells, we should expect to find them in the third division, but here not even a cell-plate was seen. Besides this, the nearest phylogenetic relatives in which the first divisions of a megaspore result in a cellular structure are found among the leptosporangiate Filicales, where the heterospory is supposed to be of rather late origin, and it does not seem probable that *Peperomia* has reverted to the characters of an ancestor as remote as one in which we would find the first divisions of the megaspore giving rise to a cellular structure."

Since the separating walls occur in *Peperomia* following the first and second divisions only, in the embryo sac, and not after the third division, it is difficult if not impossible to conceive of any satisfactory homology for them, except that with the mega-

spore walls of other Angiosperms, that is, if it be admitted, as it is so generally, that megaspores occur in Angiosperms.

From these significant relations—from the origin of the embryo sac from what seems clearly a megaspore mother-cell, from the occurrence of the reduction division of its nucleus, from the tetrahedral arrangement of the first four nuclei, from the complete number in the tetrad, from the resting period following the formation of the tetrad, from the increased number of nuclei in the sac, and from the appearance of evanescent walls—from all these facts in favor of our view, together with the fact that the germination of all four megaspores and the participation of all of them in the formation of one embryo sac do not constitute valid objections to the theory, we are very strongly inclined to the view that the first four nuclei in the embryo sac of *Peperomia* are the equivalents of megaspore nuclei.

This theory of homologies is in harmony with the classifications of embryo sacs by recent workers (Ernst, 20; Coulter, 13; Samuels, 59) with regard to the number of generations of nuclei from the beginning of the reduction division to the mature sac.

TEXT FIG. 1 illustrates diagrammatically the known types of derivation of the mature embryo sac from the definitive archesporial cell. The order in which these are arranged will suggest the phylogenetic sequence in which certain chief steps in the reduction of the number of cells or nuclear divisions between the definitive archesporial cell and the mature sac may have occurred. It also indicates the number of degenerating megaspores formed, where any occur.

In the type illustrated by TEXT FIG. 1a, there are *five* cell- and nuclear generations (the first two being cell-generations, and the last three being nuclear generations) in the development from the definitive archesporial cell to the mature embryo sac, which latter is of the common eight-nucleate type. The embryo sac is here indisputably the product of one megaspore, which divides three times.

In the type illustrated by TEXT FIG. 1b, the case is similar to that in TEXT FIG. 1a, but the upper cell formed by the first division of the definitive archesporial cell does not divide further. The embryo sac here contains eight nuclei, and is again clearly the product of but one megaspore, which divides three times.

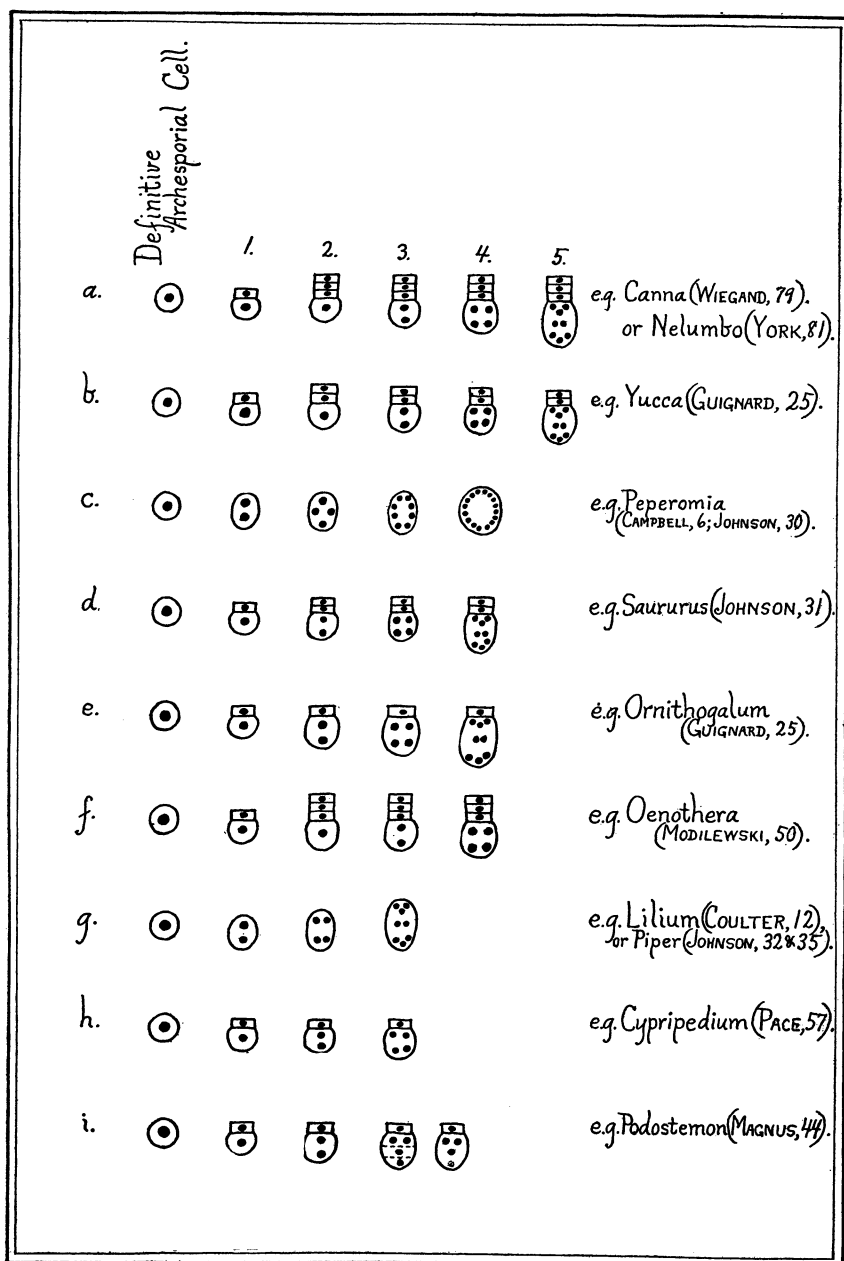


FIG. 1. Diagram illustrating the various types of embryo-sac development.

In the type illustrated by TEXT FIG. 1*c*, there are only *four* nuclear generations from the definitive archesporial cell to the mature sac. Since the first two of these nuclear divisions are followed by evanescent cell-walls, they may be regarded, as was pointed out above, as the equivalents of the first two cell-generations in TEXT FIG. 1*a*. That is, they are to be regarded as megaspore nuclei, and the mature embryo sac is the product of four megaspore nuclei, each megaspore nucleus dividing twice.

In the type illustrated by TEXT FIG. 1*d*, the definitive archesporial cell divides into an upper and a lower cell, of which the upper divides once more forming two potential megaspores, and the lower develops immediately, without the appearance of cell-walls, into an eight-nucleate embryo sac. Thus there are but *four* nuclear generations, from the definitive archesporial cell to the mature embryo sac, which is to be regarded as the product of the morphological equivalent of two megaspore nuclei.

In the type illustrated by TEXT FIG. 1*e*, there are *four* generations, one cell-generation and three nuclear generations, from the definitive archesporial cell to the mature embryo sac, which latter contains eight nuclei, and may be considered to be the product of the morphological equivalent of two megaspore nuclei, each dividing twice.

In the type illustrated by TEXT FIG. 1*f*, there are *four* generations, two cell-generations and two nuclear, from the definitive archesporial cell to the mature embryo sac. The sac here contains four nuclei and is clearly the product of one megaspore, which divides twice.

In the type illustrated by TEXT FIG. 1*g*, there are *three* nuclear generations, from the definitive archesporial cell to the mature embryo sac, which latter contains eight nuclei, and may be considered to be the product of the morphological equivalent of four megaspore nuclei, each dividing but once.

In the type illustrated by TEXT FIG. 1*h*, there are *three* generations, one cell-generation and two nuclear, between the definitive archesporial cell and the mature embryo sac, which latter contains four nuclei, and may be considered to be the product of the morphological equivalent of two megaspore nuclei, each dividing once.

In the type illustrated by TEXT FIG. 1*i*, the case is similar to

the preceding, the difference being that two evanescent cell-walls appear after the second division in the embryo sac, and that the lowest nucleus in the sac degenerates, so that the mature sac contains but three nuclei, which have arisen from the morphological equivalent of two megaspore nuclei.

If we accept this view of the phylogenetic sequence of the steps in the reduction of the development of sporogenous tissue, it is evident that *Peperomia*, as well as *Saururus*, *Ornithogalum*, and *Oenothera*, illustrates the first stage in the abbreviation of the development of megasporogenous tissue. The number of cell- or nuclear divisions from the definitive archesporial cell to the mature embryo sac has been reduced from five to four.

From the same point of view, *Piper*, as well as *Lilium*, *Cypripedium*, and *Podostemon*, illustrates the second stage in this reduction, where the number of cell or nuclear divisions from the definitive archesporial cell to the mature embryo sac has been reduced to three. This is the condition found by Yamanouchi (80) in *Fucus*, that is, the number of nuclear generations from the beginning of the reduction divisions to the mature egg is three.

As Miss Pace (57) has pointed out, if reduction should go one step further, we should have the condition present in the maturation of the animal egg. But no case showing reduction of the female sporogenous tissue to two cell-generations has been reported in plants.

It may be added that no unquestioned case of more than five cell and nuclear generations from definitive archesporial cell to mature embryo sac has been reported. Dessiatoff (16) reported a case of six cell-generations in *Euphorbia virgata*, but Modilewski (52) later got different results when working on the same species.

As has been frequently pointed out, there is much more variation in the development of embryo sacs than was formerly thought. Coulter & Chamberlain (14, p. 76, 77) call attention to the great variability in the family Liliaceae. The Podostemaceae, also, show considerable variation, as shown by Magnus (44). Sometimes the variability is very great in a single genus.

In the genus *Burmannia*, Ernst & Bernard (22, 23) found an interesting series of cases. In the species studied, the sub-epidermal primary archesporial cell becomes the definitive

archesporial cell without cutting off a parietal or tapetal cell. In *Burmattia Championii* this forms sometimes three, but usually four megaspores, and a typical eight-nucleate embryo sac develops from one of these, while the remaining two or three degenerate. In *B. candida* the definitive archesporial cell divides into two cells, the chalazal one giving rise to a typical eight-nucleate embryo sac, while the other degenerates. The division of the definitive archesporial cell is the heterotypic reduction division; therefore, the cell which gives rise to the embryo sac is the morphological equivalent of two megaspores. In *B. coelestis*, as a rule, the definitive archesporial cell develops directly into the embryo sac, without cutting off any non-functional megaspores. A typical eight-nucleate embryo sac is developed here from the morphological equivalent of four megaspores. It is interesting to note here that the end product in all three cases is a typical eight-nucleate sac, whether it is developed from one megaspore or from the morphological equivalent of two or of four megaspores.

In the genus *Euphorbia*, two species, *E. procera* and *E. palustris*, both investigated by Modilewski (49, 51, 52), have sixteen-nucleate embryo sacs, while at least thirteen other species of the same genus, investigated by the same author, have typical eight-nucleate embryo sacs. The latter condition was also found in *Ricinus*, *Phyllanthus*, *Securinega*, and *Croton*, four related genera belonging to the same family, the Euphorbiaceae.

Within a single species there is sometimes striking variation, as in *Epipactis pubescens* (Brown & Sharp, 5), where usually the embryo sac arises from the innermost one of three megaspores, but in other cases four megaspores take part in the formation of the sac. The authors further state that there is some evidence that the embryo sac may at times be derived from two megaspores. In *Salix glaucophylla* (Chamberlain, 11) there is even greater variation than in *Epipactis pubescens*.

That the origin of the embryo sac from the morphological equivalents of four megaspores as found in *Peperomia* is a derived condition rather than primitive, is further indicated by the following considerations:

(1) The vast majority of the embryo sacs of Angiosperms arise from a single megaspore, and the exceptions are not limited

to plants which for other reasons are known to be primitive. The sixteen-nucleate sacs, which have almost certainly arisen from four megaspores, are distributed among four families of dicotyledonous plants, the Piperaceae, the Haloragidaceae, the Penaeaceae, and the Euphorbiaceae, none of which except the first has been considered primitive.

The eight-nucleate embryo sacs, which have arisen from four megaspores or their morphological equivalents, are found in widely separated families of both monocotyledonous and dicotyledonous plants. They occur in *Typha* (Typhaceae) according to Schaffner (61), in *Lemna* (Lemnaceae) according to Caldwell (8), in *Lilium* (Liliaceae) according to Coulter (12), in *Epipactis* (Orchidaceae) according to Brown & Sharp (5), in *Piper* (Piperaceae) according to Johnson (32, 35), in *Salix* (Salicaceae) according to Chamberlain (11), in *Juglans* (Juglandaceae) according to Karsten (38), in *Avicennia* (Verbenaceae) according to Treub (77), and in *Aphyllon* (Orobanchaceae) according to Miss Smith (67).

While it may be doubted whether the embryo sac is the product of four megaspores or their morphological equivalents in all cases mentioned above, it certainly can not be doubted in cases like *Epipactis* (Brown & Sharp, 5) and *Smilacina* (McAllister, 45).

(2) In none of the heterosporous plants below the Angiosperms is the gametophyte known to be the product of the fusion of four germinating megaspores.

The endosperm nucleus of *Peperomia* in its origin from several nuclei shows a derived rather than a primitive condition, for nothing of this kind is found in other Angiosperms which are considered primitive, or in the heterosporous plants below the Angiosperms.

The endosperm of *Peperomia*, which is cellular from the start, exhibits in this condition a feature which is secondary rather than a characteristic that is primitive among Angiosperms.

The primary archesporial cell, which is single in *Peperomia*, represents a less primitive condition, according to Körnicke (40), than the multicellular archesporium which is found very much more commonly among the more primitive of the Dicotyledons than among the higher groups. The evidence for this view has also been briefly reviewed by Coulter & Chamberlain (14, p. 60).

Representatives of all four families of the order Piperales have been examined in an attempt to ascertain whether any species showed an intermediate stage between the embryo sac of *Peperomia* and that of the typical eight-nucleate embryo sac, and to see whether any feature of the development of the embryo sac confirmed the view that *Peperomia* is primitive.

Of the Piperaceae, besides the genus *Peperomia*, four species of *Piper* have been examined—three by Johnson (32, 35) and one by the writer and reported in this paper. All four have been shown to have eight-nucleate sacs, which develop directly from the definitive archesporial cell, no non-functional megaspores being formed. No other condition has been found in this genus. As was pointed out, the reduction in the number of generations, from the definitive archesporial cell to the mature embryo sac, has proceeded one step further in this genus than it has in the *Peperomia*.

Of the Saururaceae, species of *Saururus*, *Anemiopsis*, and *Houttuynia* have been examined by Johnson (31, 33), and *Houttuynia* by Shibata & Miyake (66), and it is found that one or more non-functional megaspores are cut off and that in all cases typical eight-nucleate embryo sacs are formed from single megaspores.

Of the Lacistemaceae, *Lacistema* (Johnson, 33) shows a typical eight-nucleate embryo sac derived from a single megaspore.

Of the Chloranthaceae, *Hedyosmum* (Johnson, 33) and *Chloranthus* (Armour, 1) have been examined, each of which shows a typical eight-nucleate embryo sac which arises from a single megaspore.

A mode of origin and development of the embryo sac, which would confirm the idea that *Peperomia* is primitive, has not yet been found in any other genus of the order Piperales.

Finally, when we consider, (1) that the primary archesporial cell of *Peperomia* is single—a condition probably derived; (2) that the first four nuclei of the embryo sac are probably homologous with megaspores, certainly not a primitive feature; (3) that the peculiar origin of the endosperm nucleus here probably represents a derived condition; (4) that an endosperm which is cellular from the start can not be regarded as primitive; and (5) that none of the close relatives of *Peperomia* furnishes any indication, from the

development of the embryo sac, that the genus is primitive, we are inclined to accept the view first advanced by Johnson (30) and since confirmed by other workers (Brown, 4; Samuels, 59) that the peculiarities in origin and development of the embryo sac of *Peperomia* have been secondarily acquired.

SUMMARY

The primary archesporial cell is single and subepidermal in all species of *Peperomia* examined.

The nucleus of the definitive archesporial cell, or embryo sac mother-cell, goes into synapsis before its first division.

Evanescient cell-walls occur following the first and second nuclear divisions in the embryo sac in all six of the species of which the material was most nearly complete.

The mature sac contains sixteen nuclei, one of which functions as the egg nucleus, one as that of the single synergid, from six to nine others fuse to form the endosperm nucleus, and the remainder are individually cut off by cell-walls about the periphery of the sac and afterwards degenerate.

The endosperm is cellular from the start.

The embryo is undifferentiated externally except for a slight flattening on the micropylar side.

In *Piper tuberculatum* we have a typical eight-nucleate embryo sac, developed directly from the definitive archesporial cell, no degenerating megaspores being formed.

That the first four nuclei in the embryo sac of *Peperomia* are homologous with megaspore nuclei, seems extremely probable from the following facts: (1) they arise from a cell which with very little doubt may be considered a megaspore mother-cell; (2) they are arranged tetrahedrally; (3) the tetrad is complete in number; (4) the larger than usual number of nuclei in the mature sac is in harmony with this view; (5) the reduction of chromosomes occurs in the divisions which give rise to these four nuclei; (6) a resting stage follows the formation of these four nuclei; and (7) evanescent cell-walls frequently follow the first and second divisions in the embryo sac, but not the third.

In view of the following considerations: (1) that the primary archesporial cell of *Peperomia* is single—a condition probably

derived; (2) that the first four nuclei of the embryo sac are probably homologous with megaspores—certainly not a primitive feature; (3) that the peculiar origin of the endosperm nucleus here probably represents a derived condition; (4) that an endosperm which is cellular from the start cannot be regarded as primitive; and (5) that none of the close relatives of *Peperomia* furnishes any indication, from the development of the embryo sac, that the genus is primitive, the writer is inclined to believe that the peculiarities in origin and development of the embryo sac of *Peperomia* have been secondarily acquired.

Finally, I wish to thank those who have helped make this study possible. I am under obligation to Dr. Charles B. Davenport, Director of the Biological Laboratory of the Brooklyn Institute of Arts and Sciences, Cold Spring Harbor, Long Island, New York, for the use of a room in the Research Laboratory of that Institution in 1911; to Captain John Donnell Smith for the use of certain books from his library; to Dr. Casimir de Candolle for determining specimens of the plants studied; to Mrs. Bessie Wiley Fisher who carefully made the majority of my slides; and to Professor D. S. Johnson who collected a large portion of the material and to whom I am also greatly indebted for helpful criticism throughout the work.

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Explanation of plates 3-6

All figures are camera drawings except FIGS. 25 and 26, and all are from microtome sections except FIGS. 25, 26, and 36. The magnification given in the description of each figure is that actually shown by the figure as printed on the page.

FIGS. 1-18. *Peperomia reflexa*

FIG. 1. Longitudinal section of nucellus showing primary archesporial cell. $\times 670$.

FIG. 2. Longitudinal section of ovule, showing definitive archesporial or embryo sac mother-cell, and parietal or tapetal cell. $\times 670$.

FIG. 3. Longitudinal section of nucellus containing mature embryo sac mother-cell and two-layered tapetum. $\times 670$.

FIG. 4. Longitudinal section of carpel showing subtending bract, nucellus, embryo sac mother-cell, integument, micropyle, stylar canal, and immature stigma. $\times 72$.

FIG. 5. Longitudinal section of definitive archesporial cell, or embryo sac mother-cell, the nucleus showing synapsis. $\times 670$.

FIG. 6. Nearly longitudinal section of a two-nucleate embryo sac showing evanescent cell-wall. $\times 670$.

FIG. 7. Longitudinal section of a four-nucleate embryo sac showing tetrahedral arrangement of the nuclei. $\times 670$.

FIG. 8. Longitudinal section of a four-nucleate embryo sac showing evanescent cell-wall. $\times 670$.

FIG. 9. Longitudinal section of an eight-nucleate embryo sac. $\times 670$.

FIG. 10. Longitudinal section of an embryo sac containing sixteen free nuclei. $\times 670$.

FIG. 11. Longitudinal section of a mature embryo sac showing group of endosperm nuclei. $\times 670$.

FIG. 12. Group of eight nuclei almost completely fused to form the endosperm nucleus (from transverse section of spike). $\times 670$.

FIG. 13. Longitudinal section of an embryo sac showing egg, two peripheral nuclei, and two-celled endosperm. $\times 670$.

FIG. 14. Longitudinal section of an embryo sac showing male nucleus within the egg, but not yet fused with the egg-nucleus, also the single synergid and the several celled endosperm. $\times 465$.

FIG. 15. An embryo showing four cells in longitudinal section; endosperm several-celled. $\times 465$.

FIG. 16. Longitudinal section of mature embryo and endosperm. $\times 300$.

FIG. 17. Longitudinal section of a mature fruit showing how far it is sunk in the axis. $\times 50$.

FIG. 18. Hydathode and hair from a transverse section of peduncle of spike. $\times 220$.

FIGS. 19-27. *Peperomia verticillata*

FIG. 19. Transverse section of pollen-sac showing tapetum and tetrads of microspores. $\times 670$.

FIG. 20. Longitudinal section of ovule showing primary archesporial cell; the integument just started. $\times 465$.

FIG. 21. Longitudinal section of an embryo sac containing sixteen free nuclei. $\times 670$.

FIG. 22. Longitudinal section of young carpel containing a lobed ovule. $\times 220$.

FIG. 23. Longitudinal section of lobed ovule, older stage than preceding. $\times 50$.

FIG. 24. Lateral exterior view of a reconstruction of a lobed ovule. $\times 80$.

FIG. 25. Median longitudinal section of the preceding, showing integument and embryo sac of the fertile lobe. $\times 80$.

FIG. 26. Transverse section of a lobed ovule, showing position of embryo sac in small fertile lobe. $\times 220$.

FIG. 27. Longitudinal section of a deformed seed developed from a lobed ovule (somewhat diagrammatic). $\times 50$.

FIGS. 28-34. *Peperomia scandens*

FIG. 28. Nearly longitudinal section of a two-nucleate embryo sac, showing the cell-plate, which is the beginning of the evanescent cell-wall. $\times 670$.

FIG. 29. Transverse section of two-nucleate embryo sac showing evanescent cell-wall. $\times 670$.

FIGS. 30, 31. Longitudinal sections of two-nucleate embryo-sacs showing evanescent cell-walls. $\times 670$.

FIG. 32. Longitudinal section of a young carpel showing how far it is sunk in the axis. $\times 50$.

FIG. 33. Longitudinal section of a mature fruit, showing how far it is sunk in the axis. $\times 50$.

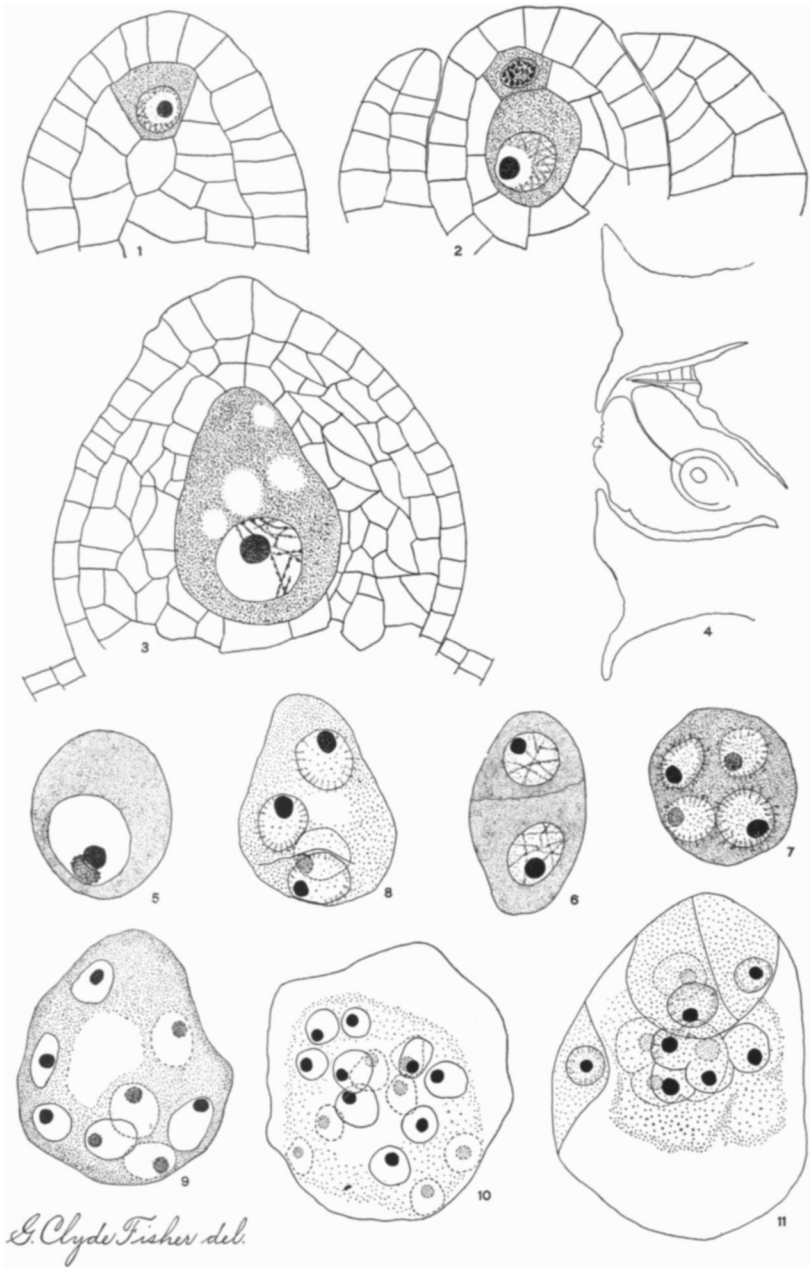
FIG. 34. Longitudinal section of the upper part of an embryo sac, showing the egg and the single synergid. $\times 670$.

FIG. 35. *Peperomia metallica*

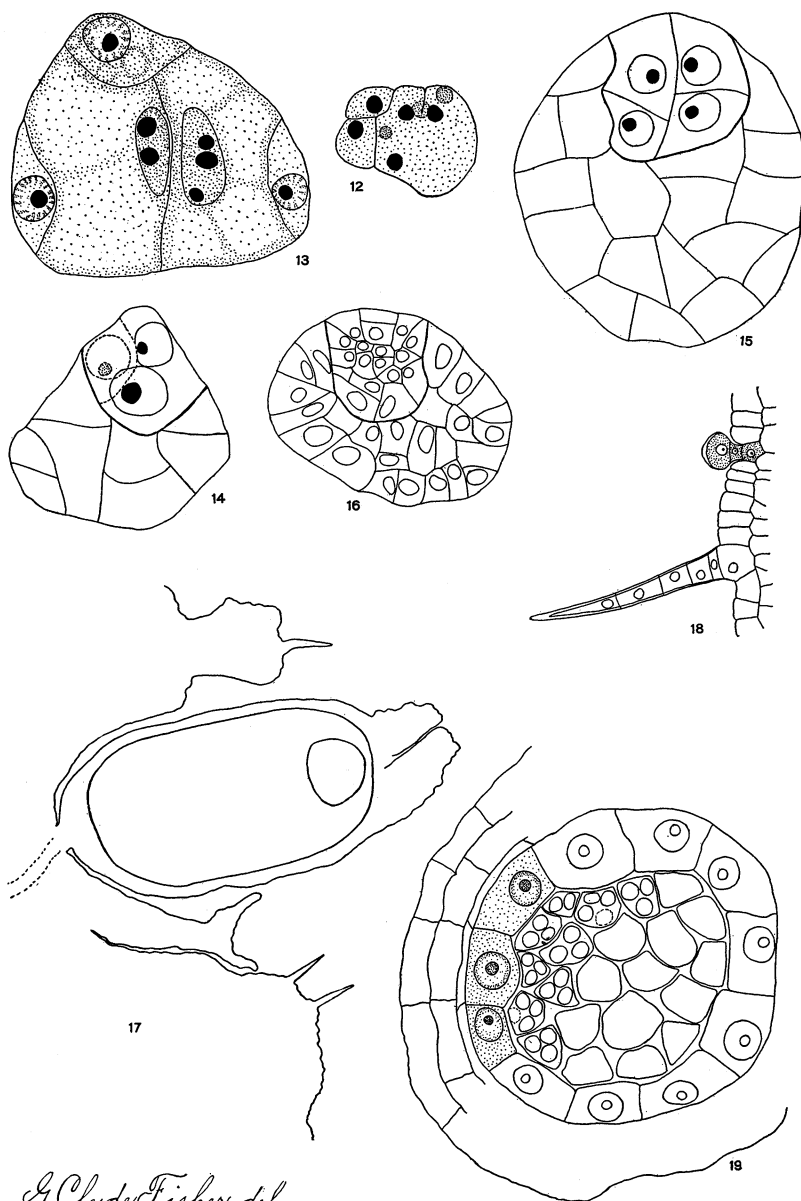
FIG. 35. Lateral view of an interrupted flower-spike, showing zone of small vegetative leaves. $\times 1$.

FIG. 36. *Peperomia blanda*

FIG. 36. Longitudinal section of a four-nucleate embryo sac, showing evanescent cell-wall. $\times 670$.

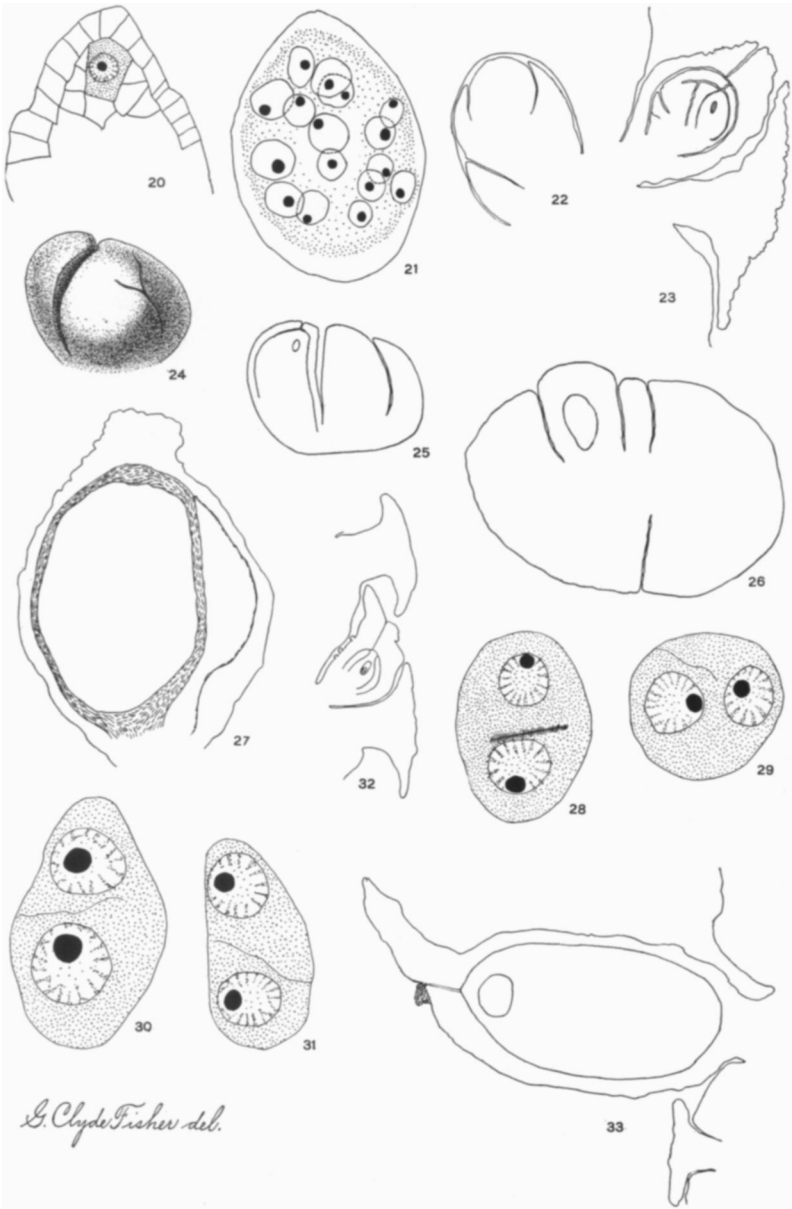


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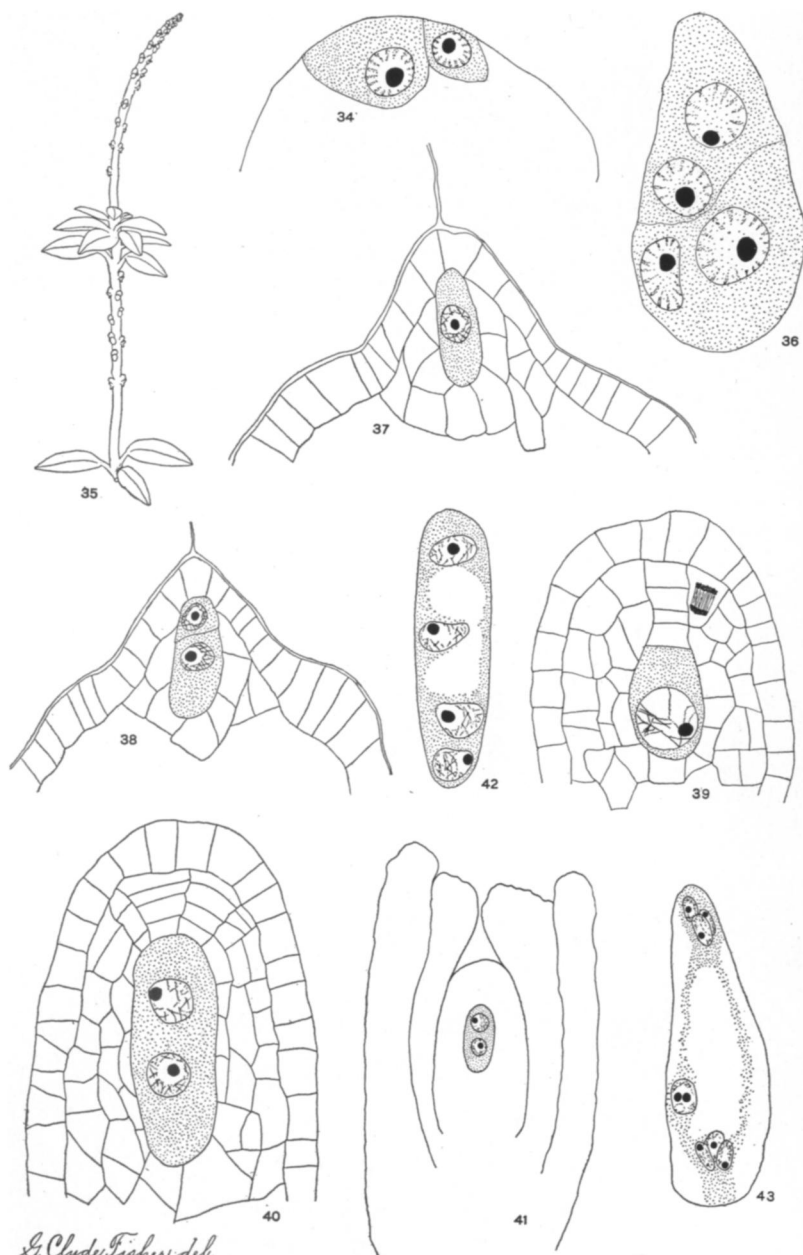


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FIGS. 37-43. *Piper tuberculatum*

FIG. 37. Longitudinal section of young ovule, showing primary archesporial cell; integuments not yet started. $\times 670$.

FIG. 38. Longitudinal section of a slightly older ovule, in which the primary archesporial cell has divided to the definitive archesporial cell and the parietal cell. $\times 670$.

FIG. 39. Longitudinal section of slightly older ovule, showing definitive archesporial cell or embryo sac mother-cell; the parietal cell has divided forming tapetum four cells thick. $\times 670$.

FIG. 40. Longitudinal section of nucellus, showing two-nucleate embryo sac. $\times 670$.

FIG. 41. Same as preceding in outline with addition of integuments. $\times 220$.

FIG. 42. Longitudinal section of four-nucleate embryo sac, showing the linear arrangement of the nuclei. $\times 670$.

FIG. 43. Longitudinal section of eight-nucleate embryo sac, the two polar nuclei fusing to form the endosperm nucleus. $\times 670$.